RESEARCH ARTICLE

Individual and temporal variability in the courtship behavior of White-ruffed Manakins (*Corapipo altera*), a species with facultative cooperative displays

Megan A. Jones,[1]* Emily H. DuVal,[1] and W. Alice Boyle[2]

[1] Department of Biological Science, Florida State University, Tallahassee, Florida
[2] Division of Biology, Kansas State University, Manhattan, Kansas
* Corresponding author: majones@bio.fsu.edu

ABSTRACT

Investigation of the ecological and evolutionary basis for the often-intriguing courtship behavior of animals requires that we understand the patterns of variation inherent in such behaviors. The courtship displays of the White-ruffed Manakin (*Corapipo altera*) are not well-known, and previously published descriptions and interpretations of displays conflict with one another. We studied the reproductive behavior of *C. altera* during 6 breeding seasons, observing 72 display courts (mean 29 ± 2.5 courts annually) for a total of 2688 hr. We updated the behavioral characterization of *C. altera* by reconciling 8 previous ethologies and describing 2 new behavioral elements, vouchering all with audio and video recordings. We evaluated evidence for the occurrence of male–male cooperation and characterized the physical attributes and temporal dynamics of displays and display courts. We found strong evidence of cooperation among males; 32% of displays for females were highly coordinated displays performed by 2 males, and 8% of those ended in copulation. Males of the highest social status (alphas) retained that status for an average of 1.7 yr (range 1.5 mo to ≥5 yr). Most alphas remained at a single court during their alpha tenure and rarely declined in social status. Only 23% of second-ranked (beta) males transitioned to alpha status, and of those 70% became alphas at a new display court. Display courts did not seem to be limited because few measured physical attributes differed between active display logs and random logs. Several elements of *C. altera* display behavior and social organization were more variable than in other manakin species, including high turnover of the display courts. This work provides key information for comparative studies investigating the evolution of cooperation in Pipridae.

Keywords: cooperation, coordination, courtship display, exploded lek, Pipridae

Variabilidad individual y temporal en el comportamiento de cortejo de *Corapipo altera*, una especie con despliegues cooperativos facultativos

RESUMEN

La investigación de las bases ecológicas y evolutivas del intrigante comportamiento de cortejo de los animales requiere que entendamos los patrones de variación inherente a tales comportamientos. Los despliegues de cortejo de *Corapipo altera* no son bien conocidos, y las descripciones previamente publicadas y las interpretaciones de los despliegues entran en conflicto entre ellas. Estudiamos el comportamiento reproductivo de *C. altera* durante seis temporadas reproductivas, observando 72 arenas de despliegue (promedio de 29 ± 2.5 arenas al año) por un total de 2688 horas. Actualizamos la caracterización del comportamentamiento de *C. altera* reconciliando ocho etologías previas y describiendo dos nuevos elementos de comportamiento documentados con grabaciones de audio y vídeo. Evaluamos la evidencia de existencia de cooperación macho-macho y caracterizamos los atributos físicos y la dinámica temporal de los despliegues y las arenas de despliegue. Encontramos fuerte evidencia de cooperación entre machos; 32% de los despliegues para las hembras fueron áltamente coordinados y hechos por dos machos, y 8% de ellos terminaron en cópula. Los machos de mayor estatus social (alfa) retuvieron su estatus por 1.7 años en promedio (de 1.5 meses a ≥5 años). La mayoría de los alfa permanecieron en una sola arena durante su tiempo como alfa, y rara vez descendieron en su estatus social. Solo 23% de los machos beta cambiaron al estatus alfa, y de ellos, el 70% llegaron a ser alfa en una nueva arena de despliegue. Las arenas de despliegue no parecieron estar limitadas ya que pocos atributos físicos medidos fueron diferentes entre los troncos de despliegue y troncos escogidos al azar. Varios elementos del comportamiento de despliegue y la organización social de *C. altera* fueron más variables que en otras especies de saltarines, incluyendo el alto recambio de las arenas de despliegue. Este trabajo provee información clave para estudios comparativos sobre la evolución de la cooperación en la familia Pipridae.

Palabras clave: cooperación, coordinación, despliegue de cortejo, lek disperso, Pipridae

INTRODUCTION

Mating systems and reproductive behaviors are central facets of a species' life history. For poorly known species, understanding the nature of reproductive tactics is a prerequisite for tackling a wide suite of ecological or evolutionary questions. Cooperative mating systems can pose particular challenges to accurately characterizing interactions because multiple individuals are involved and individual roles may vary considerably. Cooperation is intriguing because cooperating individuals engage in activities that increase another individual's fitness at an immediate cost to their own fitness (Hamilton 1964, Axelrod and Hamilton 1981, West et al. 2007, Akçay et al. 2012). One form of cooperation occurs in the context of displays that function in mate attraction, and Neotropical manakins (Aves: Pipridae) provide some of the best-known examples of cooperative display (Diaz-Muñoz et al. 2014). Understanding the factors that lead to variation within and among species in cooperation is critical for understanding the evolutionary history of cooperation within a clade and addressing comparative questions about the evolution of cooperative behaviors.

While formal definitions of cooperation involve actions that impose fitness costs, in practice quantifying individual fitness costs is rarely feasible; therefore, empirical studies often use operational definitions of cooperative display behaviors based on coordination and temporal synchrony during activities related to mate choice (Gilliard 1959, Foster 1977). Display coalitions have been defined as those involving (i) 2 or more individuals at the same time at the same court; and (ii) synchronization between males in the timing, location, and nature of the displays. Furthermore, for coalitions to be deemed cooperative, the males must (iii) attract and (iv) mate with a female during these multi-male displays (Diaz-Muñoz et al. 2014). These criteria provide a more tractable basis for identifying cooperation when directly estimating the fitness payoffs of different behaviors is impractical.

Courtship behaviors of species in Pipridae include obligate solitary displays, facultative cooperative displays, and obligate cooperative display coalitions. Thus, the family is an excellent clade in which to understand the causes of variation in reproductive strategies (Prum 1990, 1994). Cooperative displays are exemplified by the genus *Chiroxiphia* in which 2 or more males form long-term partnerships and perform highly coordinated displays. Those displays culminate in copulation for only the dominant partner (Foster 1981, McDonald 1989, DuVal 2007b), although subordinate *Chiroxiphia* do derive future benefits from cooperation (DuVal 2007a, 2013, McDonald 2009). The extent of cooperation in many other Piprid species is not known, however. In at least one other species (*Pipra filicauda*) there seems to be some individual-level

variation in coordinated display; 90% of males partnered at times, with other males, and 31% of displays were coordinated (Ryder et al. 2009, 2011). We lack detailed information on whether other species exhibit individual variation in cooperation. Elucidating the conditions under which individuals chose to cooperate vs. display solitarily would offer a novel perspective on the selective forces shaping cooperative behavior.

The existence of cooperation in the White-ruffed Manakin (*Corapipo altera*) is a matter of debate. *C. altera* displays have been categorized differently by different authors, ranging from solitary displays (Aldrich and Bole 1937, Slud 1964) to multiple male groups (Skutch 1967) or a combination thereof (Ridgely and Gwynne 1992, Rosselli et al. 2002). Likewise, studies differ in their characterization of the incidence of male–male coordination and the contexts in which males display together. A likely reason for these discrepancies is that all previous descriptions of *C. altera* courtship summarized observations of few display courts in studies of short duration ($\leq$8 courts, $\leq$1.25 mo; Table 1). Furthermore, while many behavioral elements have been described, the lack of audio or visual behavioral vouchers makes it difficult to reconcile different authors' accounts or make comparisons with better-known species. Thus, despite hints that the behavioral repertoire of this species includes individual variation required to understand the selective forces shaping cooperative behavior in manakins, the nature of mating behavior in this species has remained elusive.

Our objectives in this study were 4-fold. Using a dataset spanning 6 breeding seasons, 72 display courts, and 2688 hr of observation, we first reconciled new observations with past descriptions of reproductive behavior where possible and documented behaviors with vouchered audio and video files. Second, we evaluated the evidence for cooperation and coordination in courtship displays of *C. altera* by describing (a) novel behaviors and behavioral contexts, and (b) quantitative summaries of behavioral patterns. Third, we updated and expanded descriptions of the attributes and landscape configuration of display courts, including quantitative summaries of physical and geographic parameters. Fourth, we described the inter-annual variability in this system with regard to transience of display courts themselves and the males that display upon them. Our overarching objective in providing this comprehensive description of *C. altera* reproductive behavior is to lay the foundation for future tests of hypotheses explaining causes of variation in reproductive behavior in this species.

METHODS

Corapipo altera is a small (9–13 g), frugivorous bird distributed from southern Honduras to northern South

TABLE 1. Previous publications that present original observations of *Corapipo altera* male courtship display behavior. Other publications mention *C. altera* courtship behavior, but the list here is limited to those that present original observations.

Source	Location	n Logs	Study duration	Color-banded birds?	Multi-male description
Aldrich and Bole 1937	Azuero Peninsula, Panama	0	Few days	No	Solo only
Slud 1964	Costa Rica, location unknown	Unknown	Few days	No	Two males that never share space
Skutch 1967	Southwestern Costa Rica	4	Few days	No	Extensive, not coordinated
Skutch 1969	Costa Rica, location unknown	Unknown	Few days	No	Simultaneous behavior but not coordinated
John Rowlett (in Davis 1982)	Cerro Azul, Panama	0	1 day	No	3 males together; coordination not mentioned
Stiles and Skutch 1989	Costa Rica, location unknown	Unknown	Unknown	Unknown	Log shared by 3–4 males, but display one at a time
Ridgely and Gwynne 1992	Panama	Unknown	Unknown	Unknown	Multiple males at display court
Rosselli et al. 2002	Caribbean slope, Costa Rica	8 (intensive obs. at 4)	34 days	Few	Multiple males but not coordinated; subordinates did not display for female
This study	Caribbean slope, Costa Rica	72	6 breeding seasons	Yes; 771 birds	Solo males and multi-male display coalitions that display cooperatively

America (Skutch 1969, Stiles and Skutch 1989, Ridgely and Gwynne 1992). On the Atlantic slope in Costa Rica, the breeding season lasts from late February to mid-June, peaking in late March (M. A. Jones personal observation). Peak capture rate of recently fledged young occurs in June (Boyle 2010). During the nonbreeding season, Atlantic slope populations are partially migratory; many individuals descend to lower elevations for 3–8 months (Boyle et al. 2010). Courtship consists of complex flight displays by males, including visual and auditory components. Display courts consisting of a horizontal, moss-covered log and nearby plants (Rosselli et al. 2002) are loosely clustered in an "exploded" (or dispersed) lek in which most displaying males have some auditory contact with other displaying males (Prum 1994, Höglund and Alatalo 1995, Rosselli et al. 2002). Here we define the lek as a spatial cluster of multiple display courts; one or more males may display regularly at each court.

We observed *C. altera* from 2008 to 2013 on the adjacent private reserves of Rara Avis Rainforest Lodge and Reserve and Selvatica on the Caribbean slope of Costa Rica (10°16′54.27″N, 84°2′41.75″W). We studied *C. altera* both within a 11.5 ha research plot, gridded with narrow paths every 50 m, and more opportunistically along ~10 km of trails traversing the 485 ha combined reserves between 650 and 850 m a.s.l. (Figure 1). During the breeding seasons we identified suspected *C. altera* display courts by listening for display-specific sounds. Within the plot, we also systematically searched for groomed vegetation on moss-covered logs (see "gardening"; Table 2). We considered a court to be active when we observed a definitive-plumaged male displaying on the log. At the beginning of each breeding season, we visited all courts that had been active in any previous year. We deemed courts inactive if they were overgrown, had decayed beyond recognition, or had been destroyed by treefall. We conducted 4–6 hr of observations at courts suspected to be abandoned but that appeared useable. If no definitive-plumaged males displayed on or near the court during that time, we considered it to be inactive.

We captured *C. altera* in mist nets placed near display courts as well as at fixed capture locations monitored as part of a long-term study of the bird community. We marked each *C. altera* with a unique combination of one numbered aluminum and 1–3 colored plastic leg bands (*n* = 771 individuals; 517 males, 237 female, and 17 birds of undetermined sex). We sexed birds based on plumage (Skutch 1967), molt limit (Ryder and Duraes 2005), and interpubic bone distance (Mendenhall et al. 2010). The plumage of males in their first 13–14 mo of life and females of all ages is similar, being largely green with a grey throat. After the first complete molt as second-year (SY) birds in July–November, young males have a black mask and a partial white ruff but retain a mainly green plumage.
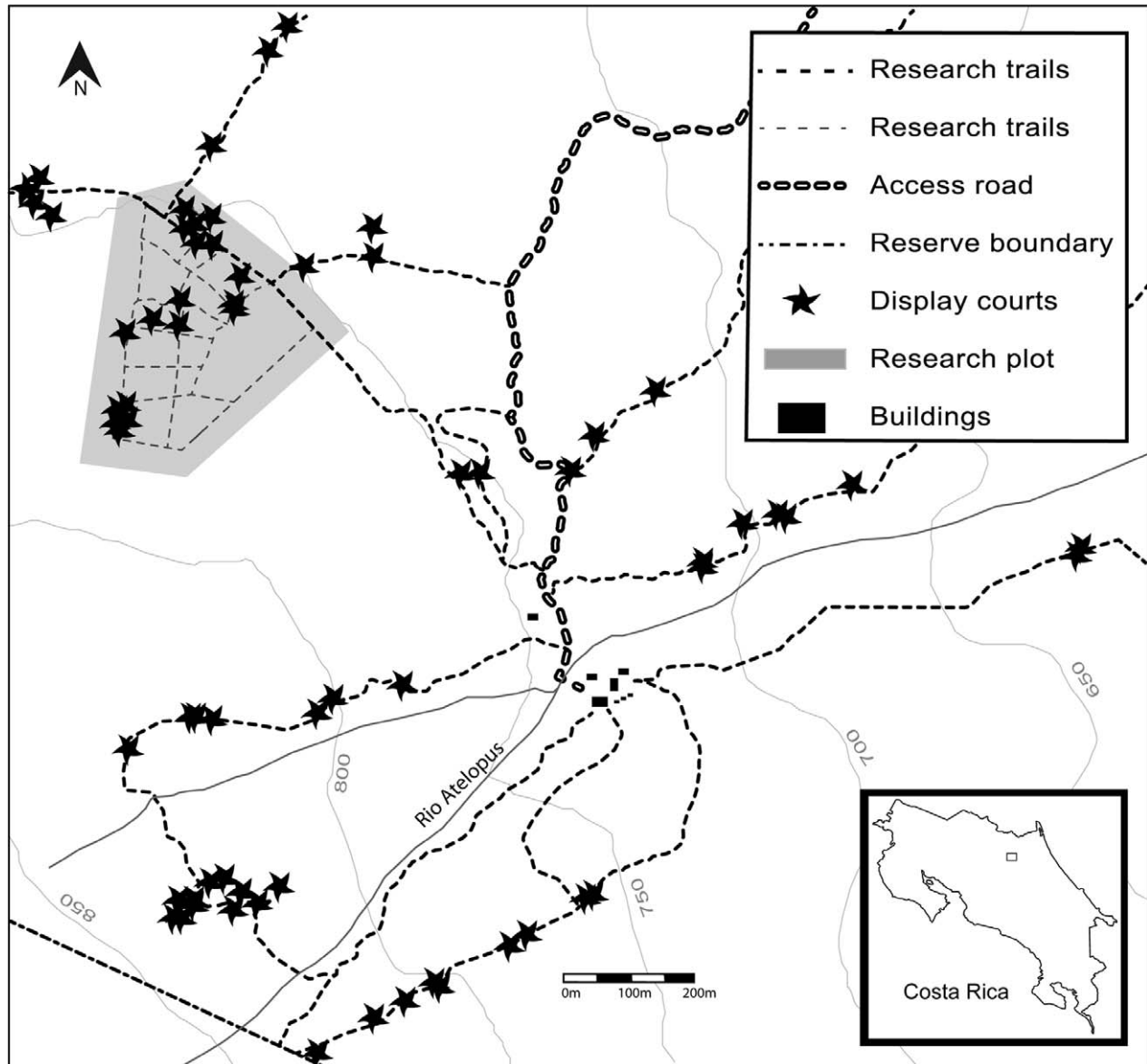
FIGURE 1. Research area on the Rara Avis and SelvaTica reserves in Costa Rica (inset map). The grey polygon delimits the research plot that was systematically searched from trails placed ~50 m apart and was used for all spatial distribution analyses. Only the main river and streams are portrayed on the map; there are numerous small streams throughout the reserves. Elevation reported in meters.

Not until their third-year (TY) molt in July–October do males achieve the glossy blue-black definitive plumage with the full white ruff. Thus, during the February–June breeding season, we were able to age males as SY, TY, or after-third-year (ATY) by plumage.

We inferred the sex of unbanded green-plumaged individuals at display courts from the reaction of definitive-plumaged (i.e. ATY) males. We assumed that birds were females if they did not display and if their presence elicited an intensification of male displays. In contrast, we assumed birds were SY males if they performed male-typical display components, did not elicit

an intensification of the display, or were chased by the ATY male. These criteria were verified during observations of known-sexed (i.e. color-banded) green birds; females always elicited an intensification of display ($n = 18$ displays with banded females in 2011–2013) whereas young males elicited little or no reaction from ATY males or actively performed male-typical displays ($n = 31$ displays with banded SY males in 2011–2013).

Observations at Display Courts
We conducted observations from camouflaged blinds placed 8–10 m from display logs. Observers noted display

types, number, and identity of displaying and attending individuals and the timing of all components of reproductive behavior. In 2008 and 2009 we conducted 3 hr observations starting at 0700 and 1200. In 2010–2013 we conducted 2 hr observations starting at 0700, 1000, and 1300. We observed active display courts at least once per week throughout the breeding season except in 2010 when we observed display courts twice per month. We observed each active court for 8–18 hr each year (mean 15 hr ± 1.6 SE), totaling 2688 hr of observations. We recorded an additional 316 hr of video at 10 courts in 2009. We placed the camera 4–8 m from courts and camouflaged it with green shade cloth and local vegetation. We recorded continuously for 5–6 hr and minimized human activity near courts being recorded. We deposited audio and video vouchers of display behavior excerpted from these recordings and accessioned them to the Macaulay Library of the Cornell Lab of Ornithology (Table 2).

Characterization of Social Rank

Our preliminary observations revealed that males at some display courts appeared to display only solitarily, whereas at other courts, we typically observed several displaying males. Thus, within each season at each display court, we characterized all males present at each display court as having 1 of 3 social ranks. The "alpha" spent the most time at the court, was most often present in the absence of other males, and vocalized most in the absence of other males. "Betas" spent a substantial amount of time (mean = 42% ± 38 of observation time, range = 5–100%) at display courts and participated in displays with the alpha on at least 2 different dates within a season; however, betas displayed and called less frequently than alphas and were rarely present in the absence of alphas. We classified males as "floaters" if they did not participate in multi-male displays but visited display logs on at least 2 dates within a season.

Observers assigned social ranks following each observation session based on an integrated but subjective interpretation of the relative activity, behavior, and the duration that each male was present during the observation. At each display court we identified a season-long alpha (and, when applicable, a beta) based on the proportion of observations each male was ranked as the alpha at that court. In addition to this qualitative assignment, we quantitatively assigned status categories in 2011–2013. We based quantitative ranks on the same presence and activity criteria, but we summed quantitative ranks across observations within each season. In all instances, the qualitative and quantitative rankings matched during the 3-yr period during which we employed both methods.

We noted the number and type of all elements of *C. altera* displays, assigning elements to a new display bout when 1 min passed without activity at the court. We classified displays as "multi-male" displays when 2 or more ATY males performed simultaneously on the court. "Displays for female" were those occurring any time a female *C. altera* was detected at the display court. Although we only include displays by ATYs in our assessment of cooperation and coordination, we also discuss the incidence of display behaviors by younger males. Displays of a SY or TY male occurred alone or in the presence of other males of any age but never in the presence of a female.

Criteria Defining Cooperative Display Coalitions

To address our second objective of assessing the evidence for cooperation in *C. altera*, we summarized the types and social context of display behaviors. We evaluated these behaviors in light of 7 proposed criteria for identifying cooperative display coalitions: (i) 2 or more males are involved; (ii) synchronization between males in coordinated displays that function in (iii) mate attraction and (iv) copulation contexts (Diaz-Muñoz et al. 2014); and whether (v) unique behaviors were performed only when 2 or more males interact (Prum 1990), (vi) there were established dominance hierarchies between males (Prum 1990), and (vii) multi-male displays were an obligate part of copulation (McDonald 1989). We tested for differences in the likelihood that single vs. multi-male displays ended in copulation using a generalized linear mixed model (GLMM) with male identity as a random factor, implemented in the "lmer" of package lme4 in R (R Core Team 2013).

Characteristics of Display Courts

We quantified the attributes and persistence of display courts of *C. altera* by measuring the log diameter (at the location where displays were concentrated) and classifying log type (dead woody log, living woody trunk, dead palm, living liana, or living root). To document change in the logs over time, we photographed all active and inactive logs in each year of the study. Additionally, in 2011 we quantified the attributes of active and inactive (formerly active) courts relative to physical resources available in the area by pairing active courts with randomly selected non-display logs. We selected non-display logs by following a random compass direction from the display court until encountering a log ≥10 cm diameter, ≥0.75 m length, and ≤30° slope. These size and slope criteria were based on minimum dimensions and maximum slopes of 60 actively used logs measured in prior years. Several courts were located along the reserve trails. In such cases, we did not follow a random direction but paired display logs with the nearest log meeting the size and slope criteria along the same trail in a randomly selected up- or down-trail direction.

TABLE 2. Primary elements of *Corapipo altera* as described in this paper and matched to descriptions in previous papers. Numbers denote description references: [1] Aldrich and Bole 1937, [2] Slud 1964, [3] Skutch 1967, [4] Davis 1982, [5] Prum 1990 (numbers, <x>, refer to characters as specified in [5]), [6] Prum 1998, and [7] Rosselli et al. 2002. Here we present a concise description of each behavior (Description), the context in which it occurs (Context), and note where previous publications differ from these descriptions (Discrepancies). Catalog numbers refer to video or audio clips of each behavior archived with and accessible through the Macauley Library. *Continued on next page.*

Display element	Terms used in previous papers	Description
Trill (TR)	"See" [3], advertisement call or trill [7]	
Emphatic trill (ET)	"Sree" or "sreeir" [2], little squeals [3], warble or "nuurt" call [7]	
Seew-seew calls (SS)	Flight song display [4], above-the-canopy flight display [5, <38>], canopy calls [7]	A series (2–9) of thin, high-pitched calls performed above the forest canopy while male flies in a large loop
Flap-chee-wah (FCW)	"tsee-ruck" [2], flap-cheee-waaa[3], log approach display [5, <31, 34, 35>], flap-chee-wah [7]	Appears to combine a mechanical flap sound just before landing on the log with a "chee-wah" vocalization that occurs while the bird makes a short hop along the log while turning about face. Hop occurs over the female if she remains on log.
Aerial flap (AF)		Probable mechanical sound produced at low point of dive from above canopy in the vicinity of the display log
Butterfly flight (BF)	Retarded flutter[2], bouncing flight [3], butterfly display [5, <26, 37>], butterfly flight and undulating flight [7]	Short flights around the display court in which the bird's body position is in a near vertical orientation
Log landing (LL)	Described but not specifically named	Individual (male or female) lands on log, most often on groomed landing pad
Throat flag (TF)	Described [2, 3]; hunched posture [5, <5>], wing-shiver log display [5, <3, 16:wing shiver>], and throat feathers erect [5, <6>]; throat flagging [7]	The male performing a stylized crouch while erecting his white throat feathers
Rapid flights (RF)	Seen performed by SY bird [3], "modulated mechanical sound during noisy flights"[6], rapid flights [7]	Low, quick, short flights between near perches; flights often audible as steady whirr
Partner pursuits (PP)	Described [2, 3], chases [7]	Two males engage in rapid, low stylized "chase" around court separated from each other by ~1 m. Males perch next to each other after flight
Aggressive pursuits (AP)	Attack behavior [7]	Alpha chases another male in a straight, upward flight away from display court; alpha returns alone
Gardening	Gardening [7]	Male uses bill to trim or groom vegetation and moss on or around the display log

At paired display and non-display logs we measured diameter and slope, and canopy cover using a concave spherical densiometer (Lemmon 1956). Because the display for *C. altera* involves flight from above the canopy to the display log, we also estimated an index of the size of the largest canopy gap visible from the log by counting the number of square units that reflected the gap on the spherical densiometer (hereafter densiometer units). A key food for *C. altera* during the breeding season is *Miconia punctata* (Melastomataceae; Boyle 2010); thus, we measured the distance from log to the closest *M. punctata* of reproductive size. To calculate an index of visual obstruction and vegetation density surrounding the court, we used a 0.5 × 0.5 m board painted in a 5 × 5 cm black-and-white grid held vertically at the point of concentrated display on the log. We estimated the area of the board visible at 1 m above the ground from distances of 2 m and 6 m in the 4 cardinal directions. We then averaged the 4 directional estimates separately for the 2 m and 6 m distances to obtain 2 indices of vegetation density surrounding the log. We measured attributes of display logs from the center of the area used most heavily by males during display (the "landing pad"). We measured non-display logs at the center of the log.

Males alter the vegetation on and near display logs by trimming moss and other vegetation with their bill. To determine the magnitude of the effect of this behavior on log characteristics, we compared the difference in height of moss and other vegetation on display logs and randomly paired logs in 2012. We used different random logs from those used for vegetation sampling but selected random logs using the methods described above.

TABLE 2. *Continued.*

Display element	Discrepancies	Context	Catalog numbers
Trill (TR)		Males; many contexts; primary call of alpha male at display court	190863
Emphatic trill (ET)	Given by either sex [2]	Males; typically in presence of other males at or away from display court	190864
Seew-seew calls (SS)		Males; preceding AF or FCW	190865, 190866, 473506, 473507, 473508
Flap-chee-wah (FCW)		Males; alone or in presence of males or females. Preceded 44 of 45 copulations	190866, 473506, 473507
Aerial flap (AF)	Males give flap sound while perched [3]	Males; when alone or with males	190865, 473508
Butterfly flight (BF)	Humming sound and periodic "tiny explosions" [1], "tseee" when landing on log; performing FCW (or tsee-ruck) upon landing on the log [2]	Males; in presence of females or other males	473509
Log landing (LL)		Males; solo or in presence of males or females; accompanies BF, TF, or gardening. Females; usually results in escalation of male display; required for copulation	473510, 473511, 473512
Throat flag (TF)		Males; alone or in presences of males or females	473513
Rapid flights (RF)	RFs with a subdued snap or pop in flight on landing [7]	Males; most often in presence of females before rest of display initiated	473514
Partner pursuits (PP)	Interpreted as aggressive behavior [5,7]	Two males simultaneously; in presence of males or females.	473515
Aggressive pursuits (AP)	Included a "grraah or cuaak" vocalization [7]	Males; alpha male chases other male away from court, other male does not return	
Gardening		Male; when solo	473516

Density and Distribution of Courts

Rosselli et al. (2002) reported a density of 0.5 courts ha^{-1} and described courts as being spatially aggregated. To the best of our knowledge, Rosselli et al.'s (2002) 8 display courts constitute the only spatial data available characterizing *C. altera* as having an exploded lek mating system. Consequently, we determined the coordinates of each display court using a Garmin eTrex GPS, averaging >250 readings to achieve an accuracy of ≤3 m. We calculated the density of courts only within the research plot because we did not exhaustively search off trails outside of this area (Figure 1). We quantified the spatial aggregation of the courts ways using Ripley's *K* in ArcGIS 10.0 (Environmental Systems Research Institute, Redlands, CA) to detect deviations from spatial homogeneity by comparing the distribution of nearest neighbor distances to a Poisson distribution, which is the null expectation for random (non-clumped) points in space (Ripley 1988).

Persistence of Display Courts and Male Tenure

In many species of Pipridae, display courts are active for multiple years, even when the individuals attending them change (Durães et al. 2008). In *Chiroxiphia lanceolata*, display areas can be active for >15 yr, even

if individual display perches within that area are only active for a few years (E. H. DuVal personal communication), and *Manacus manacus* lek sites may be active for 42 yr or longer (Berres 2002). Because no similar information was available for courts of *C. altera*, we calculated annual turnover of the display logs themselves and characterized the patterns in log attributes and possible causes of abandonment (e.g., treefall or decay). We also characterized the temporal patterns of male tenure at individual display courts. Our estimates represent minimum values of court persistence and male tenure duration because many courts were active before the start or remained active at the conclusion of our study.

To estimate turnover rates of display courts, we calculated the mean proportion of active courts in each year that ceased to be active in the following year. For active courts, we then summarized the proportions of transitions from active to 3 types of inactive courts: those abandoned by ATY males but used by younger males, those abandoned by all *C. altera* but still apparently intact, or those destroyed. We also constructed Kaplan-Meier survival curves for display logs to estimate mean log persistence times, accounting for the fact that logs still

active at the conclusion of this study represent censored observations.

We characterized patterns of male tenure in several ways. First, for males that were observed as alphas in one or more years, we calculated total or minimum tenure duration (for males whose alpha status overlapped the beginning or end of the study). We estimated turnover rates as the proportion of active courts having a different alpha than in the previous year. We then quantified the proportions of these transitions in which the new alpha male was (a) previously an alpha at a different court, (b) beta at the same court, (c) beta at a different court, (d) a floater, or (e) an unknown individual. Finally, we determined the average length of beta tenure prior to becoming alpha and the proportion of betas that we eventually observed to become alphas.

RESULTS

Over the 6 years of this study, we found 72 courts (Figure 1) and conducted 2688 hr of observation. In each year, 21–38 courts (mean 29 ± 2.5) were deemed "active" (i.e. used by a displaying ATY male). ATY males used 67 courts in >1 yr. During the 6 years, we observed 221 banded males and 34 banded females at display courts (mean 59.7 ± 11 males and 8.7 ± 3 females per year). Most females observed at display courts were not banded; however, female visits were not uncommon. We observed 436 individual visits lasting a combined total of 35.9 hr (1.6% of total observation duration), and we witnessed 43 copulations. Individual ATY males visited an average of 1.24 ± 0.49 display courts each year (range 1–3 display courts). At each log, we observed on average 1.52 ± 1.59 ATY males (range 1–7) in each year. These estimates are minimum values because they were calculated based on observations of known males at known display courts; at each display court where ≥1 unbanded males were observed, only a single male was included in the calculation even though more than one unbanded male may have been observed. Younger males (i.e. SY and TY) regularly displayed on logs alone (0.18 displays hr^{-1} of observation in 2011–2013), with other young males (0.13 displays hr^{-1}), or in groups of both younger and ATY males (0.07 displays hr^{-1}). We never observed females at display courts while young males were displaying.

Updated and Amended Ethogram of Male Display
We compiled a list of the courtship behaviors of *C. altera* and a reconciliation of the various terminology, details, and attributed function of behavioral elements used by previous authors (Table 2). We observed 2 previously undescribed behaviors. First, males performed the same non-vocal "flap" sound that occurs during the *flap-chee-wah* at the low point of the dive when still high in the

canopy (Macaulay Library Catalog Number 190865, 473508). These *aerial flaps* occurred at varying heights ranging from just above the display log to mid-canopy or in a canopy gap near the court. As in the *flap-chee-wah*, display *seew-seew calls* generally preceded the *aerial flap*. Males typically perched near the display court but did not land on the log following an *aerial flap*. Second, we confirmed rare female vocalizations (Macaulay Library Catalog Number 190867). We noted calls by banded, known females in 3 contexts: (1) occasionally during banding while a female was being handled by a researcher; (2) twice when a female was perched on display log but no male was present; (3) and ≥3 times while a female was seemingly interacting with an ATY male at a fruiting tree.

Our observations of *C. altera* behavior differed from previous reports in 4 key respects (Table 2). (1) We never heard a "plop" or "flap" sound associated with *rapid flights* or *butterfly flights* (contra Aldrich and Bole 1937, Rosselli et al. 2002). (2) During a *throat flag*, the bird's body was generally oriented perpendicular to the direction of the log, not parallel as described in Rosselli et al. (2002), although the male's head was frequently rotated toward a nearby bird on the log (Figure 2B). (3) We never observed males making a "flap" sound while perched (contra Skutch 1967). (4) No previous authors had described direct observations of birds while they produced *seew-seew calls*. Although rare, through gaps in the canopy we observed displaying males producing these calls. Males produced the *seew-seew calls* generally ≥4 m above the canopy and sometimes up to 2 times the canopy height. The flight dynamics appeared labored with a body position similar to, but not as pronounced as the *butterfly flights*. Males produced the calls while flying in a horizontal plane above the canopy, not on the ascent or descent as noted in Davis (1982). We infrequently heard *seew-seew calls* away from display areas, contra Rosselli et al. (2002).

Our interpretation of some displays involving multiple males also differs from previous accounts. First, Skutch (1967) and Rosselli et al. (2002) interpreted *partner pursuits* as an aggressive chase by a dominant male. *Partner pursuits* involved 2 males flying rapidly at a near-constant elevation, weaving through and around understory vegetation in a ~20 m radius around the display court. We interpret these flights as a component of multi-male displays rather than aggressive interactions for several reasons. First, they were common; we observed 0.24 ± 0.21 *partner pursuits* hr^{-1}. One male followed the other at a distance of ~1–1.5 m in rapid flights lasting from a few seconds to up to 5 min. Second, individuals frequently changed roles. While we could rarely determine the identity of both leading and following individuals, some *partner pursuits* involved both a green pre-definitive male and a blue-black ATY male (e.g., see Macaulay Library Catalog Number 473515). Thus, we were able to
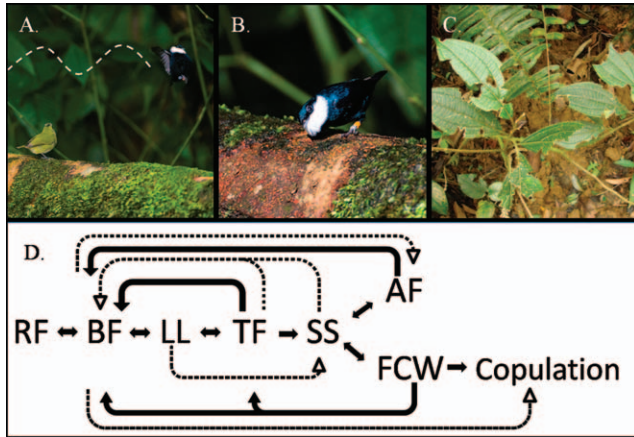
FIGURE 2. The progression of *Corapipo altera* courtship displays is variable, but typically begins with (**A**) *rapid flights* (RF) or *butterfly flights* (BF), then proceeds to (**B**) *log landings* (LL) and *throat flags* (TF). Any of these elements may revert to BF or proceed to *seew-seew calls* (SS). *Aerial flaps* (AF) or *flap-chee-wahs* (FCW) follow SS and copulations are almost always preceded by FCW. (**C**) Areas near display logs often have ragged leaves due to males biting at vegetation surrounding the display court (gardening). (**D**) Typical progression of courtship displays is shown with solid arrows, and observed alternative transitions between display elements are shown by dashed arrows.

determine that individuals switched between "leading" and "following" roles. Third, individuals seemed to tolerate each other when not engaged in *partner pursuits*; following such flights, both males often perched near to one another in the display court, seemingly unagitated by the other's presence.

Another line of evidence suggesting that *partner pursuits* did not function in agonistic interactions came from our observations of *aggressive pursuits*, characterized by the alpha male chasing another, presumably intruding, male in rapid, direct flights up and away from the log. These *aggressive pursuits* occurred infrequently ($0.02 \ hr^{-1}$), and we were never able to determine the identity of the male being chased away. Following *aggressive pursuits*, only the alpha returned to the display court. *Aggressive pursuits* seem to be analogous to what Rosselli et al. (2002) termed "attack behavior," but we never heard the "*grraaahh*" or "*cuaak*" sound accompanying such attacks.

Coordination and Cooperation

We observed behaviors involving multiple males that were consistent with the definition of cooperative display coalitions (criteria i–iv, as listed in methods) and previously described cooperation in Pipridae (criteria v–vii). First, we frequently observed 2 or more ATY male *C. altera* displaying together in a court (criterion i) and landing on the log simultaneously or sequentially without apparent antagonistic interactions (Figure 3 and Macaulay Library Catalog Numbers 4713511, 473517). In 2011–
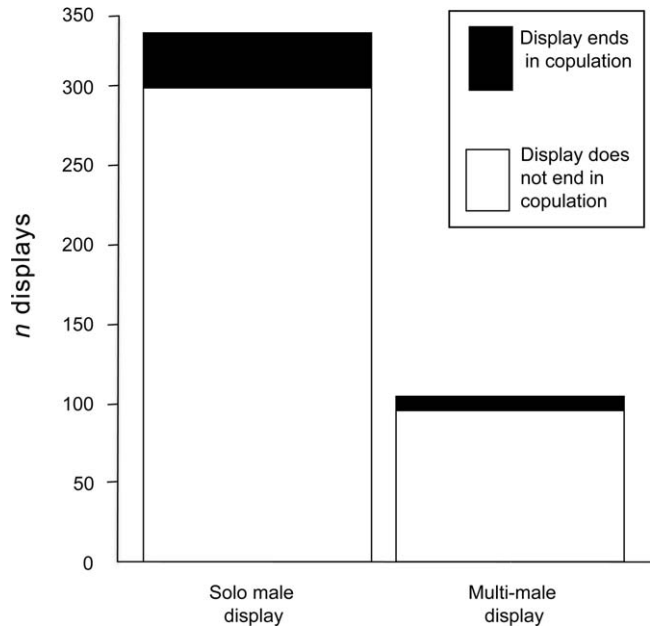
FIGURE 3. Adult male *Corapipo altera* primarily displayed solo for females (76.3% of displays for females) but also display in cooperative partnerships. There was no significant difference in the likelihood of a solo or a multi-male display ending in a copulation (GLMM with random effect of male identity, intercept 0.46 ± 0.84, $z = -0.32$, $P = 0.59$).

2013, we observed multiple ATY males displaying together during 12.2% of 498 observations during which at least one individual was seen, and 57.5% of 106 observations during which we detected ≥ 2 ATY males. All precopulatory behaviors performed by a single male were also performed together by 2 males, with the exception of gardening.

Consistent with the second major criterion for cooperative displays, we observed males performing display behaviors synchronized in time and place. Two or more males performed *butterfly flights* to, from, and across the display log in the presence of females and without a female present. These flights occurred either at the same time in different directions, or in succession, frequently with both males flying in the same sequence of directions. Multiple males also landed on the log and *throat flagged* simultaneously (see Macaulay Library Catalog Number 473517). Displaying males often alternated roles in a series of *flap-chee-wah* displays during which one male would *flap-chee-wah* over or next to another male and then remain on the log while the other male would do the same (also described in Rosselli et al. 2002). During the final component of the *flap-chee-wah* display, males hopped from the initial point of contact with the log to another location along the log (within ∼30 cm of first). If a female was present on the log, the males leaped over the female. Our videos of multi-male *flap-chee-wah* displays reveal that the "stationary" male often coordinates a leap in

synchrony with the diving male in the opposite direction along the log (see Macaulay Library Catalog Number 473517).

Multi-male displays also functioned in the context of mate attraction. Our extensive observational dataset revealed that multi-male displays does frequently occur for females (criterion iii) and could result in copulations (criterion iv; Figure 3). Displays performed by 2 males were not more likely than one-male displays to end in copulation (GLMM with random effect of male identity, intercept -0.46 ± 0.84, z $= -0.32$, $P = 0.59$; Figure 3). Disruption of copulation by another ATY male was rare (one instance in addition to the 45 successful copulations observed).

We also observed a unique cooperative behavior (criterion v). *Partner pursuits* only occurred when 2 or more males were present; we did not witness analogous flights of single males. Partner pursuits occurred both in the presence and absence of females. Consistent with criterion vi, many males maintained stable dominance hierarchies with other males as assessed by social status category, at least within breeding seasons. We observed males interacting in season-long alpha–beta relationships at 24.6% of 167 court-year combinations. Most (90% of 41) partnerships between males lasted only a single season while 4 partnerships lasted 2 seasons. In the year following each of these four 2-year partnerships, at least one male in each partnership disappeared (i.e. was never subsequently captured or observed).

The only behavioral criterion describing other highly cooperative species in Pipridae that *C. altera* did not display was that cooperation was not obligatory for copulation to occur (criterion vii; Figure 3). Solitary male displays were frequent and effective in attracting females to display courts. Thus, cooperative display occurs but is highly facultative in this species.

Characteristics of Display Courts

Corapipo altera used a variety of substrates for display (Figure 4). Of the 62 courts used by ATY males, 44 (72.6%) were fallen dead trunks of angiosperm trees as described previously (Skutch 1967, Rosselli et al. 2002); however, *C. altera* also displayed on dead fallen palms (7 courts, 11.3%), exposed living tree roots (7 courts, 11.3%), and horizontal live woody tree trunks (3 courts, 4.8%). The diameter of logs active in 2011 averaged 19.5 cm (median 16.5 cm, range 7–52 cm, $n = 31$). At the 2 m distance, 80.2% (median 81.6%, range 40–100%) of the primary display portion of active courts were visible, declining to 36.1% (median 36.3%, range 0.5–82.5%) at 6 m. The mean slope of active logs was 10° (median 9°, range 0–35°), and canopy cover was nearly complete (median 93.8%, range 83.5–97.7%); the average largest gap in the canopy was 1.8 densiometer units (median 1.3, range 0–8).

To determine if *C. altera* males select logs having nonrandom attributes, we compared active ($n = 11$, 5 on trails), formerly active ($n = 15$, 7 on trails), and paired random logs. Log diameter, slope, vegetation at 2 m and 6 m, canopy density, and size of largest canopy gap did not differ between active, formerly active, or random logs (all comparisons, Welch's *t*-tests, $P > 0.18$). Active *C. altera* display logs were covered with moss that was on average 2.4 mm shorter than on inactive logs (Kruskal-Wallis test, $\chi^2 = 10.4$, df $= 1$, $P = 0.001$) and 4 mm shorter than on random logs (Kruskal-Wallis test, $\chi^2 = 4.2$, df $= 1$, $P = 0.04$). These results suggest that gardening behavior of males is effective at modifying moss and vegetation height on the display pad, but that males are not highly selective for the log characteristics we measured.

Spatial Density and Distribution of Courts

Over the 6-yr period, we found 16 display courts within the 11.5 ha research plot resulting in a density of 1.4 courts ha^{-1} (Figure 1). The mean density of active logs in each year was 0.6 ± 0.1 courts ha^{-1}, or 0.7 ± 0.1 courts ha^{-1} when we included logs used only by young males. The distribution of distances between display courts was above the 95% confidence envelope of a Poisson distribution for distances of 10–13 m and 30–33 m, demonstrating significant clustering at these distances (Ripley's $K_{10} = 28.45$, $K_{30} = 56.91$, $P < 0.05$). Within the research plot we visually identified 4 clusters of 3, 4, 5, and 6 logs each active in ≥ 1 yr. Within each cluster, the average nearest neighbor distance between courts was 26.3 m (range 11.8–47.4 m), within the range predicted from Ripley's *K*. The average distance between clusters was 145.9 m (range 132.5–165.6 m).

Persistence of Display Courts

Between 60.5% (2009–2010) and 80.8% (2011–2012) of courts used by ATY males in one year were active in the subsequent year. When logs ceased to be used by displaying ATY males (i.e. became "inactive"), they met one or more of 3 fates. Some logs were used exclusively by groups of younger (i.e. SY and/or TY) males. Other logs were destroyed (overtopped by dense understory vegetation, covered by large fallen palm fronds, or decayed beyond recognition), were washed away in floods, or were obliterated by catastrophic tree falls common at this location (Figure 4B). Many logs were abandoned for no obvious reason, however, still being apparently suitable as display logs. No log characterized as having been destroyed was ever reclaimed by displaying males (Figure 5). Active logs had a 71.9% chance of being active in the next year. We did observe 3 transitions back to active ATY use following a year of inactivity or use by only younger males. Display logs of *C. altera* were relatively transient. On average, logs remained active for 2.98 yr $\pm$ 0.20 based on

FIGURE 4. Photo series of 3 *Corapipo altera* display courts showing changes in display logs over time. (**A**) Example of a log that remained active for 6 years (photos taken in 2008, 2011, and 2013). (**B**) Example of a log that became inactive after being overgrown by vegetation (photos taken in 2009, 2011, and 2013; log last active in 2009). (**C**) Example of a log that became inactive after advanced decay (photos taken in 2009, 2011, and 2012; log last active in 2010).

Kaplan-Meier survival curves. Only 7 logs (11%) remained active over all 6 years of the study. Our dataset included too few logs to model mean survival time as a function of log type (i.e. root, living trunk, palm, or dead log) or log fate.

Persistence of Male Ownership

We identified 119 color-banded males holding the rank of either alpha ($n = 86$) or beta ($n = 33$) in at least one year and 210 transitions in social status (Figure 6). Males held alpha status at a given log for an average of 1.69 yr, with 56.8% of males being alpha for only one season. Tenure duration ranged from 1.5 mo to $\geq$5 yr. Because many birds were alphas at the beginning and/or end of the study, these values may underestimate tenure duration of successful males. Mean tenure duration of males for whom we knew the start and end of their status as alphas was 1.35 yr. Most alphas remained at a single court for all years of their tenure. Of 109 individual-year transitions where the display court was observed in prior year, annual turnover in the alpha social status at a given log was 56%, including transitions by 9.2% of alphas who switched courts; 9 males were alphas at 2 courts, and 2 males were alphas at 3 courts.

More than half of the betas (57.9% of 38 beta transitions) and nearly half of the alphas (44.5% of 128 alpha
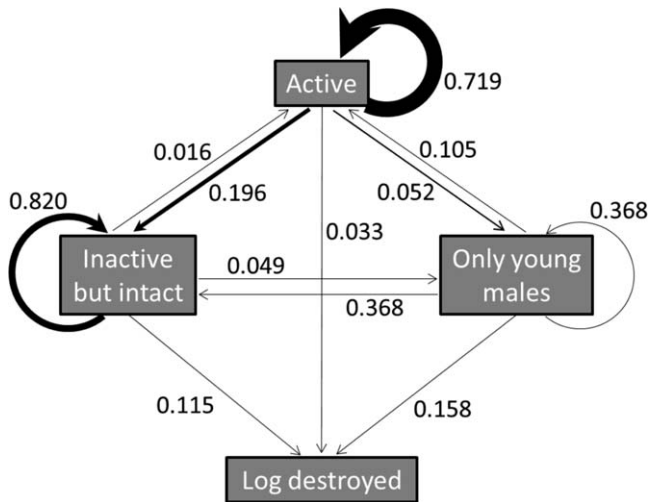
FIGURE 5. Summary of the fates of display logs "active" during this study (i.e. displayed upon by after-third-year [ATY] males). Numbers beside arrows depict the proportion of transitions between states; active, inactive but apparently intact, abandoned by ATY males but used by younger males, and complete destruction. No logs ever returned to active use by males of any age following destruction. Widths of arrows are proportional to the raw number of each type of transition we observed out of 233 possible transitions (consecutive log-years, excluding logs once they were destroyed).

transitions) observed in a given year were never observed again. Status of birds both increased ($n = 86$ birds) and, more rarely, declined (9 of 87 transitions where social status was known before and after transition; alpha to beta, 2 birds; alpha to floater, 5 birds; beta to floater, 2 birds). Only 5% of known-rank individuals (5 alphas and 2 betas) were captured or observed following their final year of known alpha or beta status. These individuals may have moved to display courts out of the study area or returned to floater status. Most transitions occurred between breeding seasons; however, within a breeding season, 3 alphas switched courts, 2 betas assumed the rank of alpha, and 1 alpha became a beta at a different court.

Of the 41 males initially identified as betas, 23% ($n = 10$) eventually became alphas, but only 3 of those transitions occurred at the same log (Figure 6). Among males that later became alphas, the average length of beta tenure was 1.3 yr $\pm$ 0.6, which does not differ significantly from the beta tenure of betas that did not become alphas (1.1 yr $\pm$ 0.3, $n = 28$, Wilcoxon Rank Sum, $W = 139$, $P = 0.55$; results did not change when restricted to individuals with exact tenure known). Average alpha tenure also did not differ between those that had been observed as betas (2.04 yr $\pm$ 1.1, $n = 11$ alphas) and those who were never observed to be beta (1.63 yr $\pm$ 1.0, $n = 76$ alphas, Wilcoxon Rank Sum, $W = 324$, $P = 0.19$; results did not change when restricted to individuals with exact tenure duration known).
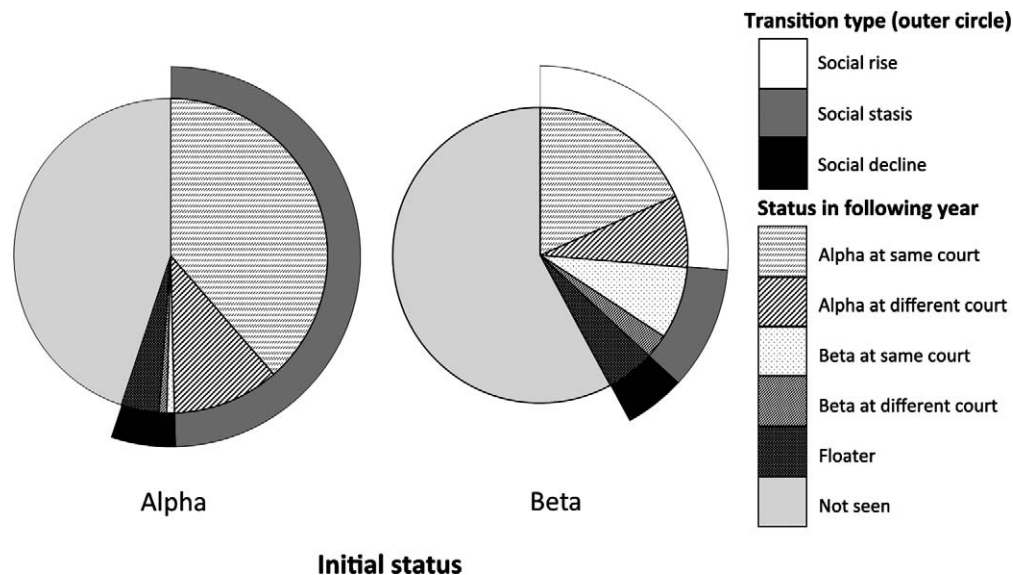
FIGURE 6. *Corapipo altera* males frequently transitioned between social ranks between breeding seasons. The transition type (social rise, stasis, or decline) is shown by the narrow, outer semicircle, and the social status in the following year is shown by the inner circle of each chart. Males of alpha status were most likely to retain their current status (grey outer circle); however, there were rare incidents of social decline (black outer circle). Males that were beta were most likely to increase in status (white outer circle) or remain at the same status (grey outer circle). Regardless of status or transition type, males were most likely to remain at the same display court instead of moving courts. Males not seen in the subsequent year (grey inner circle) were not assigned a transition type (no outer circle).

DISCUSSION

Accurate description of complex behavior is required to answer detailed comparative questions about the evolution and ecological context of such behavior. This study represents the most comprehensive investigation of *C. altera* reproductive behavior to date and provides novel insight into the details and contexts of male–male interactions in a species with facultative cooperative displays. We report extreme variability in virtually all aspects of the examined reproductive biology, which may account for some of the discrepancies among previous studies in this species. Our work increases by an order of magnitude the data assessed to characterize reproductive displays (i.e. number of display courts, number of individuals, number of years, and hours of observation; Table 1).

Differences in Descriptions of Display Behavior Among Studies

A primary goal of this study was to reconcile previous, conflicting behavioral descriptions of *C. altera*. Our attempts were hampered in some cases by confusion over terms and differences in the detail of those descriptions. Technology now exists for future studies to provide behavioral vouchers in the form of video, still photography, and audio recording to facilitate species-level and comparative research. We encourage other researchers to accompany new descriptions of behavior with similar behavioral vouchers to allow direct comparison of behavioral differences among populations and species.

A striking and important difference between our findings and previous descriptions of *C. altera* behavior lies in the interpretation of multi-male displays. We described coordination between males and evidence that multi-male displays functioned in a cooperative mate-attraction context. The basis for this interpretation stems from the frequency, stability, and synchrony of multi-male displays; interpretation of partner pursuits as cooperative rather than aggressive behaviors; and the mate attraction context of multi-male displays. While it seems certain that multi-male behavior is coordinated and functions in a cooperative context, we acknowledge that some of the same behaviors may also function in a competitive context, especially in maintaining or establishing dominance hierarchies.

While we excluded displays of young males from most analyses, 3 aspects of young male behavior merit discussion. First, multi-male displays are common in young birds (Figure 3, Macaulay Library Catalog Number 473519). Our data do not shed light on the function of such behavior, but we hypothesize that displays of SY and TY birds may serve to perfect elements of displays and develop social bonds. Young males often performed incomplete or faulty displays (e.g., missing the log, and incomplete or quiet auditory components of the *flap-chee-waa*). Interestingly, ATY males often participated in or observed these multi-male, mixed-age displays, suggesting the possibility of social learning. Although anecdotal evidence suggests that practice may be common in other species of manakins, the process by which young males learn displays is a largely neglected area of research.

Second, although pre-definitive-plumaged males have been characterized as sexually mature based on developed gonads (Aldrich and Bole 1937), we never observed young males displaying in the presence of females. Differences in migratory tendency among young males of different ages also suggest that until males achieve definitive plumage, they have little or no chance of mating (Boyle 2008, Boyle et al. 2011); migration away from breeding sites is least common among males in their TY who, for the first time in the subsequent breeding season, will have definitive adult plumage. Because residency seems to be associated with elevated risk of mortality, these age-related differences in migration suggest that reproductive benefits of residency are strongest for young adult males (Boyle et al. 2011).

Third, like previous authors (Aldrich and Bole 1937, Slud 1964, Skutch 1967), we observed groups of adult males and green birds moving and foraging together in small flocks, previously interpreted as mixed groups of females and males. Skutch (1967) first supposed these "drifting bands" to be courtship gatherings. Incidental observations of color-banded birds suggest that although females may forage in the same trees as males, "drifting bands" consist only of males of varying ages. Slud (1964) mentions males and females giving "sree" or "sreeir" vocalizations (*emphatic trill* in Table 2); however, given other details of Slud's (1964) description, we think it likely that these observations were of a mixed group of ATY and young males rather than females, a behavior we commonly observed both close to display courts and distant from them in fruiting trees. The female vocalizations we observed were more similar to the male trill than to the *emphatic trill*.

Authors of previous descriptions of *C. altera* behavior describe several instances of hearing other sounds during the displays that we did not observe during our study, although our sampling effort was an order of magnitude greater than in previous studies (6 breeding seasons vs. up to 6 weeks; see Discrepancies, Table 2). Most of the behaviors we did not observe involved an apparent nonvocal sound produced ("hum" or "snap") while the bird was perched or just approaching a perch. That some behaviors were not detected despite thorough sampling during the breeding season suggests that some fine-scale aspects of the display may vary among *C. altera* populations. Given the suggestion that Fisherian processes

may account for some of the diversity of the manakin clade (Prum 1997), population-level variation in the targets of sexual selection could be an interesting area for future work. We note, however, that during limited observations in a separate population in southwestern Costa Rica we also failed to detect the sounds reported elsewhere.

One behavior we observed but did not systematically study was a "wing-shiver" most often performed by males perched on a branch or the display log, often while in the *throat flag* position (observable in Macaulay Library Catalog Number 473512; Prum 1990). Anecdotal observation suggests that these wing flicks may be more common when displays are increasing in intensity.

Attributes of Display Courts and Leks

Results of spatial analyses were consistent with *C. altera* having exploded leks. Males were typically in auditory but not visual contact between display courts, as suggested but not quantified by previous studies (Prum 1994, Rosselli et al. 2002). This is similar to other coordinated and cooperative species within Pipridae (Foster 1981, McDonald 1989, DuVal 2007b).

Corapipo altera used a wide variety of log types, diameters, and slopes. We found no evidence that log attributes at display courts differed from other logs in the forest understory. Obstructing vegetation directly over the display court was not measured but may be more important than log characteristics in determining display locations. The remarkable lack of selectivity of *C. altera* was shown when a maintenance crew removed a trail-side display log, and males readily displayed on a new log we placed in the same location. Personal observations suggest that *C. altera* courts are not located in areas of the densest understory vegetation at our study area. Our methods restricted comparisons to a relatively small area of forest around the active display courts; therefore, our inferences are limited to this scale. While *C. altera* seem not be choosing logs based on the attributes we measured, they may choose locations of courts based on larger-scale landscape attributes or forest structure.

Temporal Dynamics of Display Courts

Display courts remained active for relatively short duration (<3 yr, with only 11% of logs active for ≥6 yr). Data are limited on longevity of individual display courts in other species of Pipridae, but in *Chiroxiphia linearis*, 82.8% of dance perches were active for >7 yr (McDonald 1989). In contrast to the variability in persistence of the display courts, the leks were stable across the years, a pattern seen in other Pipridae species (Snow 1962, McDonald 1989, Tello 2001, Loiselle et al. 2007). We observed 3 instances of birds holding alpha or beta status at an overgrown or decayed log moving to a new log within a few meters of the original log. Displays for females in the first year of activity

at the new log were often initiated on the previously active log before moving to the new log. The tenure of *C. altera* alpha males at display logs was also highly variable (0–5+ yr). The average duration of male tenure was shorter in *C. altera* than in several species of *Chiroxiphia* manakin (McDonald 2010). Additionally, yearly turnover rates (66.5%) of alpha male *C. altera* were higher than those of other manakin species, including *Pipra erythrocephala* (25–50% per year; Lill 1976) and *Lepidixthrix coronata* (32% turnover in ownership; Durães et al. 2008), indicating a relatively dynamic social hierarchy among male *C. altera*.

Variability in *C. altera* Reproductive Behavior

Virtually all aspects of *C. altera* behavior, social dynamics, attributes and persistence of display courts, and male social status were remarkably variable compared to other well-characterized species in the Pipridae. For example, the succession of events leading up to copulation varied to some degree (Figure 2D); one copulation was preceded not by the typical *flap-chee-wah* display but by a *butterfly flight*. Displays for females were more likely to follow the progression outlined in Figure 2D and to include all or most of the display elements. In contrast, displays where only males were present were often limited to few display elements, included extended pauses between elements, or transitioned between display elements without progression toward a *flap-chee-wah* culmination. This suggests that displays in the absence of females may function as practice of the individual display elements or that individual elements are more important for maintenance of social hierarchy than is the complete display.

Males displayed on logs that varied widely in physical attributes, from roots of living trees to large, decaying tree trunks or palms, all of varying slopes, heights above the ground, and diameters. Active display courts were transient in space and time with high interannual variability in which courts were used by ATY males and high rates of log decay and destruction.

The causes of high variability in this system are not known. We offer 2 possible explanations, both related to environmental differences between the montane, pluvial forest inhabited by this population and the drier and/or lower elevation forest in which the majority of other studies of manakin behavior have taken place. The first explanation relies on the consequences of high rainfall (i.e. >8000 mm yr^{-1}) for forest structure and dynamics, resulting in prolific epiphyte growth which, in combination with steep slopes, results in high rates of branch and tree falls. These falls accounted for the demise of several display courts during our study, and light gaps created by nearby tree falls resulted in growth of understory vegetation that overtopped other display logs. High rainfall also likely speeds rates of decay that accounted for the destruction of remaining logs. Thus, climatic factors may create variabil-

ity in the system by reducing the temporal and spatial predictability of display courts themselves.

A second possible explanation for variability in this system lies in the survival costs of living in an extremely wet montane environment. Partial migration in this population of *C. altera* is thought to result from starvation risk during heavy rainfall events during the nonbreeding season (Boyle et al. 2010). We thus predict that adult survival is likely to be lower in this population than in many other species of Pipridae. A shorter lifespan may select for a more flexible mating system. Furthermore, migration may limit the benefits of or ability to establish and maintain lasting partnerships and stable social hierarchies among males. Thus, it is possible that environment could constrain the evolution of highly cooperative behaviors. Few other well-studied species of Pipridae live in such wet, montane environments as do *C. altera*. It would be valuable to test the association between mating system and environmental selective pressures in both intraspecific and comparative contexts.

The insights resulting from this study highlight the value of extended studies of reproductive behavior. In dynamic systems like that of *C. altera,* short-term studies fail to capture the full extent of behavioral variability, limiting their value for comparative studies. Additionally, multi-year studies provide the basis for hypothesis-driven tests of the relationship between reproductive behavior and climate or population size.

One main objective of compiling this comprehensive description of *C. altera* reproductive behavior was to lay the foundation for future tests of hypotheses explaining the causes of variation in reproductive behavior in this species. In the genus *Chiroxiphia*, the future fitness of subordinate males is increased through their current cooperative partnership (DuVal 2007a, McDonald 2007), yet questions remain regarding the fitness consequences of cooperation to dominant individuals as well subordinates (Buston and Balshine 2007). Facultative cooperative displays, such as those observed in *C. altera*, are ideal systems in which to elucidate the costs and benefits to both partners.

ACKNOWLEDGMENTS

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